EFFECTS OF DEFOLIATION ON GROWTH OF CERTAIN CONIFERS

A SUMMARY OF RESEARCH LITERATURE

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FOREWORD

In planning forest management of spruce-fir forests in the Northeast, the possibility of recurring epidemics of the spruce budworm (Archips fumiferana) must be considered. Investigations of this insect must take into account not only the effects of defoliation on mortality, but also the growth losses that result from partial defoliation.

This report of a search of the extensive literature on defoliation is published because of its bearing on the problem. This report is limited to a summary of the work reported in important references on the subject. It contains no original data.

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by

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Defoliation by insect pests has often resulted in heavy mortality in the forests of North America. Among the more notable offenders and their coniferous hosts are the spruce budworm on spruce and balsam fir, the pine butterfly on ponderosa pine, the gypsy moth on white pine, the hemlock looper on hemlock, the tussock moth on douglas-fir, and the larch sawfly on tamarack. Under favorable conditions these insects can build up to epidemic proportions and sweep disastrously through millions of acres of valuable timber. Defoliation by forest fires and needle-cast fungi also cause mortality in conifers.

Trees that undergo partial defoliation insufficient to cause death suffer a consequent reduction in growth, because of the smaller quantities of food materials produced. This phenomenon, although less spectacular than mortality, is nevertheless important.

Defoliation By Spruce Budworm

Swaine and Craighead (18)[2] point out that during the spruce budworm outbreak of 1909-13 in Canada the trees that survived suffered a loss of 3 to 5 years' increment. From observations made during a budworm infestation, Craighead (6) observed that the growth of annual rings

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[1]Stationed at the Northeastern Forest Experiment Station's Adirondack Branch, Paul Smiths, N. Y., which is maintained in cooperation with Paul Smith's College.

[2]Numbers in parentheses refer to Literature Cited, page 11.

showed different degrees of retardation in different portions of the crown. The first year of a budworm attack on both spruce and balsam fir is characterized by a severe reduction of growth in the top of the tree, no noticeable change in the middle, and a rather decided increase near the base. In red spruce this effect is not so pronounced as in balsam fir, and in large blocks of nearly pure black spruce the first affected ring is 1 year later than in balsam.

There may be a second depression or reduction in growth because of the prolific production of cones immediately after the budworms stop feeding. Continued defoliation by the budworms for several years is marked by a rapid decline in the growth of all parts of the tree. "In both spruce and balsam the greatest reduction in the terminal and basal sections takes place the same year, in spruce 4 years after the first feeding, in balsam 5."

Following a spruce budworm attack with its resultant defoliation, an almost total suppression of rings was commonly observed in balsam, and occasionally as much as 3 years' growth was lacking on certain portions of the trunk. The spruce that recovered showed no indication of missing growth rings, but recovery of both spruce and balsam to their normal growth rates preceding the attack took 12 to 15 years.

Another interesting aspect of the last budworm outbreak in Canada was that many of the trees that survived and lived through the worst years of defoliation died 6 to 10 years later. These trees had all regained their normal amounts of foliage, but never attained their normal growth rate, as shown by the narrow annual rings. Craighead (6) reports that an extensive study of these trees was made by W. E. Hiley (School of Forestry, Oxford, England), who concluded that they were dying from a lack of rings large enough to transport required amounts of water to the crown.

Craighead (6) also noted that shortly after the defoliation of balsam fir by the budworm, the absorbing rootlets began to die; the number of dead rootlets bore a marked correlation to the severity of the defoliation. On red spruce, however, the death of these rootlets was a much more gradual process.

Closely integrated with the death of these small roots is the correlation that exists between the recovery of trees following defoliation and the amount of water available. Surveys show a higher percentage of living spruce and balsam along streams, in depressions, and on soils having a high water-retaining capacity; whereas on thin, shallow, sandy soils the death rate following defoliation is always higher.

Winter-killing is common among severely defoliated trees. The ability to withstand freezing temperatures is associated largely with the concentration of the cell sap, and trees that have been severely

defoliated cannot manufacture sufficient food to maintain high concentrations of cell sap.

All these observations on defoliation by the spruce budworm tend to point out that the vigor or vitality of a stand at the time of severe budworm attack determines to a large extent how that stand will survive. Young, vigorous growing stock stands a much better chance of survival than old, overmature timber; and it is on the basis of this that much of our present experimental budworm control work is being carried on.

Defoliation By Other Insects

Following the 1922 outbreak of the pine butterfly on ponderosa pine in Idaho, Evenden (10) reported that defoliation by this insect resulted in a marked reduction in the basal growth of all 100 sample trees, with 91 percent failing to add any basal increment. This period of no basal growth occurred in 96 percent of the trees that succumbed and 89 percent of the trees that recovered, and it varied in length from 1 to 11 years with an average of 2.6 years..

Evenden (10) and Craighead (6) agree that vigor, as expressed by basal increment, has a definite influence on the recovery of injured

Table 1.--Relation of defoliation by gypsy moth to diameter increment of white pine, 1912-21[1]

Degree of defoliation[2] (mean percent)	Trees	Decline (from average) in radial increment[3]
	Number	Percent
0-20	268	25
21-40	17	21
41-60	32	41
61-80	20	52
81-100	12	38

[1] Mean d.b.h. of white pine in 1912, 10.7 in.
[2] Dominant trees only.
[3] Includes decline from all causes. Decline from causes other than defoliation is practically constant since the same trees were used in all defoliation classes.

trees, the degree of defoliation, however, being the most important factor governing their subsequent death or recovery.

The gypsy moth is primarily a defoliator of hardwoods, but has been known to cause as much as 30 percent mortality in stands of heavily damaged young white pine. From his observations on the effects of gypsy moth defoliation on the growth of white pine, Baker (1) reported the existence of a direct correlation between the degree of defoliation and the decline in radial growth. As shown in table 1, the decline in radial increment was 52 percent greater on white pine that were 81-100 percent defoliated than in those that were defoliated 20 percent or less.

Since the greatest decline in radial increment took place in the 61-80 percent defoliated group, it is probable that the more lightly defoliated trees represented average conditions. The surviving trees in the most heavily defoliated class represented the most vigorous and resistant individuals, because the majority of white pines of this size are killed by a single complete defoliation.

The hemlock looper infestation in Oregon, which became epidemic in 1945, ran as high as 4 million loopers to the acre and resulted in the death of 40 million feet of timber before effective control measures were employed (14). Since the big consideration was to stop the ravages of this pest and prevent further mortality, partial defoliation and loss of increment were small factors.

In 1928, however, an outbreak of the hemlock looper occurred in the spruce-fir forests of Quebec, north of the Gulf of St. Lawrence. Watson (19) reported that a number of heavily defoliated balsam firs exhibited no suppression of ring growth at the end of the first year of feeding. The full effect of the 1928 feeding was not apparent until the following year, when the 1929 ring showed a marked reduction, even in those trees that did not undergo any further defoliation that year.

During the looper infestation, the growth of spruce remained normal, since only the small trees suffered any defoliation. Further studies on the reduced increment of balsam fir were made in 1930, the results of which are illustrated in figure 1.

The relatively slow growth of balsam fir in the Trinity River section is due to the fact that the trees from which the measurements were taken were growing in a muskeg, associated with black spruce. These trees were killed in 1928 without any apparent reduction in increment.

The Douglas-fir tussock moth is another defoliator that builds up to epidemic proportions and causes widespread damage. The Canadian Forest Insect Survey (5) reports that from observations made during former outbreaks, it appears that trees completely defoliated will die, and in many cases parts of trees that have been stripped fail to recover.

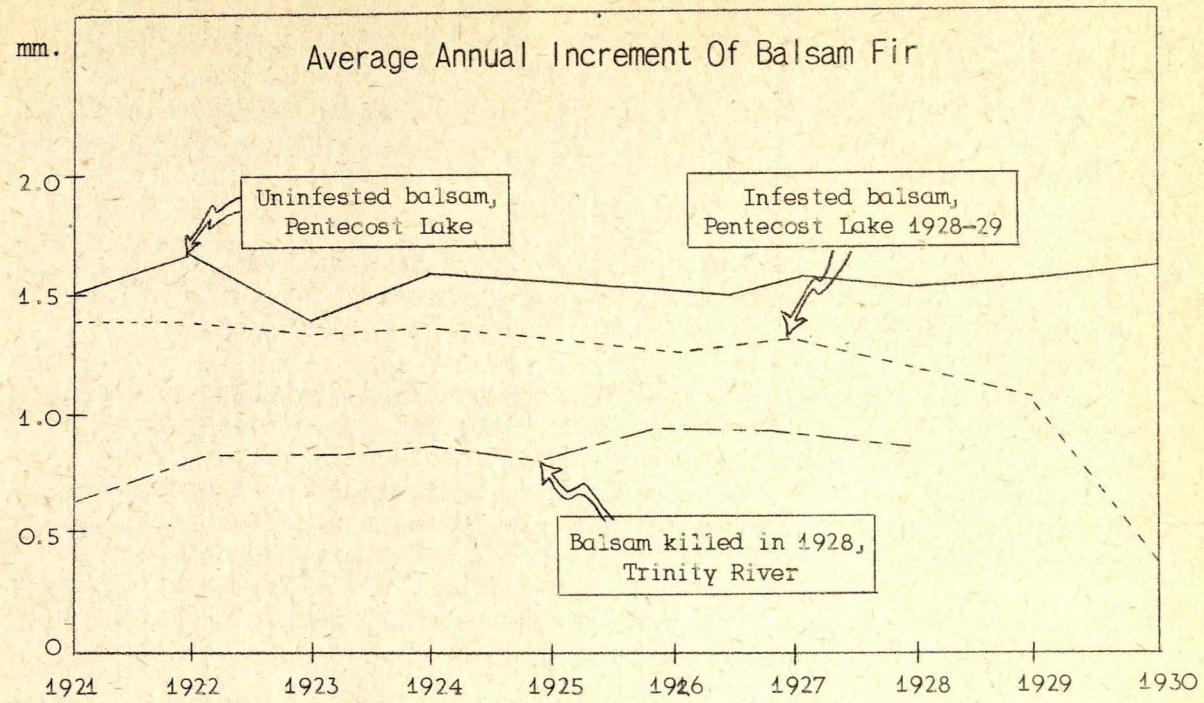

Figure 1.--Hemlock looper damage to balsam fir, as reported by Watson (19).

The first indication of reduced growth due to defoliation by the larch sawfly is reported by Harper (12) to be the absence of thickened tracheids in the autumn wood. Later there is a reduction in the width of annual rings and, in some instances, increment in the basal portion of the tree may be nonexistent. Although the growth may be insignificant at the base of the tree, there is an annual ring formed in the crown every year until death.

The fact that defoliation of the crown by insect attack immediately diminishes the increment has also been established by Büsgen and Münch (4). They point out that the scanty amount of assimilated material in partially defoliated trees is extracted from the descending sap stream in the upper part of the stem, and in the lower portion growth is practically at a standstill.

These investigators report that, in conifers, the needles of former years must assist in producing the spring shoots. Spruces completely defoliated by caterpillars in the summer invariably die because their reserve materials can produce only weak shoots inadequate to nourish the tree. Pines, if defoliated late in the season, can retain their vitality better by the production of substitute shoots, but only at the expense of reserve materials. Gradual recovery of these trees may manifest itself in the production of short "brush shoots" the summer

following defoliation, and by long shoots with few needles during the second summer.

Defoliation By Fire

Most fires in coniferous stands result in a reduced leaf area either from heat defoliation, which causes a gradual shedding of the needles, or from direct scorching and destruction by flames.

Certain types of forest fires were noted by Craighead (7) to produce characteristic growth-ring patterns that are, in many ways, similar to those produced by several leaf-feeding insects. Cross sections from a number of ponderosa pines that withstood a midsummer fire indicated that reduction in basal increment was proportional to the amount of defoliation suffered by the tree. Certain trees failed to add any wood in the lower stem for two seasons, while in the crown these effects were less pronounced. These growth characteristics are similar to those observed by Craighead (6) in his observations on the spruce budworm.

Observations of fire damage in the California pine forests by Show and Kotok (15) also substantiate the fact that reduction in diameter growth is proportional to the percentage of the crown killed by fire. Table 2 illustrates this point, data being taken from increment borings of several species 5 years after the burn.

Table 2.--Effect of crown injury on rate of growth

Amount of crown killed (percent)	Reduction of diameter growth	Basis	
		Trees studied	Average height
	Percent	Number	Feet
17	11.0	9	68
25	28.5	12	71
33	32.0	19	68
50	39.0	10	58
67	56.5	4	57

In a study of the effect of fire on the taper of young longleaf pine, Stone (16) shows that after a moderate to severe fire with resultant defoliation of 50 percent or more, there is a marked reduction

in the next season's growth. As shown in table 3, the maximum reduction in growth takes place at breast height and below, while the ring widths at higher levels are affected only slightly. The net result is a decrease in stem taper.

Table 3.--Comparative ring widths at various heights before and after fire[1]

Height of section above ground (feet)	Tree No. 1		Tree No. 2	
	Before	After	Before	After
	Inches	Inches	Inches	Inches
4	0.20	0.02	0.22	0.11
8	.19	.04	.20	.09
12	.25	.06	.23	.12
16	.26	.08	.22	.15
20	.24	.11	.29	.18
24	.25	.12	.29	.22
28	.31	.19	--	.28

[1]Radial growth in 1936-37 in stand of young longleaf pine near Saucier, Miss., burned January 8, 1937.

The fact that reduction in growth due to defoliation by fire does not take place uniformly over the stem is in agreement with the observations on defoliation by insects, in which the greatest reduction in increment takes place in the lower portion of the tree. Similar results were noticed by Cummings (9) following pruning in a young shortleaf pine plantation. For two growing seasons following pruning, there was a marked reduction in diameter growth at the 1.5- and 4.5-foot levels, but no significant difference at 7.5 feet. This decrease in diameter growth in the basal portion of the stem was due to the reduction of the living crown, as was similarly the case in defoliation by insects and fire.

Defoliation By Fungi And Hail

In addition to insects and fire, there are several other agencies of defoliation that are responsible for less extensive damage. One of these is hail, which, according to Stone and Smith (17) has been known

to defoliate trees partially or wholly and to break through the bark of small branches. Their observations of hail damage in a young stand of longleaf pine indicate that severe defoliation retards diameter growth. One particular storm, on April 30, 1937, occurred after most of the springwood had formed, but the effects of defoliation took effect immediately and only a narrow band of summerwood was laid down during the remainder of that year. In 1938 the springwood zone was much less than normal, the summerwood exceeding it in width. The following year, ring widths indicated, the diameter growth was still considerably below normal, and the recovery from the harmful effects of defoliation would apparently be a slow process.

Another agency of defoliation is that group of needle-cast fungi that occur on pine, spruce, fir, larch, and cedar. Boyce (2) reports that the chief damage caused by these needle-cast fungi is a reduction in increment, since defoliation is rarely severe enough to kill any trees except seedlings.

Artificial Defoliation Experiment

From the foregoing observations it is clear that defoliation always results in decreased diameter growth. Such a reduction, if spread over a large area like that covered by the spruce budworm, can result in a great loss in volume. Since defoliation is so important in respect to both mortality and growth, several experiments have been made to measure its harmful effects more accurately.

In experiments on defoliation of longleaf and slash pine by fire, Harper (13) found that if more than 25 percent of the needles are destroyed by the heat of the fire, gum yields will be slightly decreased and tree growth will be retarded. Complete defoliation by burning of the needles (as in a mild crown fire) caused three times the reduction in gum yields that 100 percent defoliation by heat killing (as in a hot surface fire) caused. In all cases of complete defoliation by both the heat and flame treatments, there was subsequent development of the foliage and growth during the first season after the fire.

From his artificial-defoliation experiment on tamarack, Graham (11) made the following observations:

1. Increment is reduced in direct proportion to the amount of defoliation.

2. Partial defoliation results in a relatively gradual reduction in increment.

3. Complete defoliation results in increased growth the first year, followed by a rapid falling-off in increment. Very severe defoliation apparently stimulates the use of stored food in an attempt

to grow a new set of needles. Wood is also produced by this stimulation, most of the increased increment being added in the lower section of the stem, the upper section showing little increase or decrease.

An experiment by Craighead (8) to determine the effects of defoliation on jack pine, Scotch pine, and larch produced the following results:

1. Early spring defoliation of the new growth on the pines produced a gradual reduction in the formation of wood. Successive defoliation caused a more severe reduction in increment, especially in the upper section of the tree.

2. Late spring defoliation of the new growth killed the jack pine within two seasons, while the Scotch pine resisted better. This treatment drastically affected the production of wood; the jack pines formed only a trace of wood the following spring and then died, while one of the Scotch pines failed to produce any wood. In this study Craighead found that the reduction in wood of recovering trees was relatively more pronounced in the top than at the base. However, other investigators have observed that the greatest reduction in growth occurred in the basal part of the tree.

3. Removal of the old foliage on both Scotch pine and jack pine very early in the season was insufficient to cause mortality, but resulted in a marked reduction in ring width at the base of the tree in the years of defoliation. Trees recovered more quickly from this treatment than from that in which the new growth was removed.

4. Removal of the old foliage from both species of pine after the buds had opened resulted in even less wood being produced than treatment Number 3. The widths of the annual rings were about one-fourth that of the previous year and remained at that low level during subsequent years of defoliation. The results of treatments 3 and 4 indicate that the old needles play an important part in building up the current year's growth.

5. Complete removal of all the foliage from both Scotch pine and jack pine resulted in death the following year. Büsgen and Münch (4) substantiate this observation by pointing out that artificial defoliation of several young pines at different times of the year caused death in all cases. However, when defoliation took place after breaking of the buds, the trees produced some woody growth until their reserves of starch were used up, then they died.

According to Burke (3) a similar condition exists following the coincidental attacks of the lodgepole needle tier, which feeds on the new foliage, and the lodgepole sawfly, which eats the old foliage, the result invariably being death to lodgepole pine.

Conclusions

In conclusion it may be said that the purpose of this survey of literature was to determine whether additional research should be made on the effects of defoliation on the growth of conifers. As observed from the literature reviewed, those effects that occurred most frequently can be summed up as follows:

1. Defoliation of the crown by insects, fire, diseases, or other causes immediately diminishes the increment, the reduction in growth being directly proportional to the degree of defoliation.

2. Reduction in diameter growth due to defoliation does not take place at a uniform rate throughout the stem. In the majority of cases, the greatest reduction in diameter growth took place in the basal portion of the tree.

3. Tree vigor prior to defoliation has a definite influence on the recovery of injured trees.

The literature cited in this report is evidence of the fact that a great many field observations and experiments have been made on defoliation, and suggests that results of future study to determine its harmful effects on growth would be largely repetitious.

However, there are several aspects of defoliation that might be worth further study. Among them are these:

1. Do other species have increased growth in the basal portion of the tree in the year following fire, as was reported for spruce, fir, and larch?

2. The greatest reduction in growth following defoliation has generally been found to occur in the basal portion of the tree. What treatments and species are exceptions to this, in addition to the exception reported by Craighead for pine?

3. What other species are capable of withstanding complete defoliation by fire, as reported for longleaf and slash pines by Harper?

Results of future study on such questions will be helpful in rounding out the present knowledge of how defoliation affects the growth of conifers.

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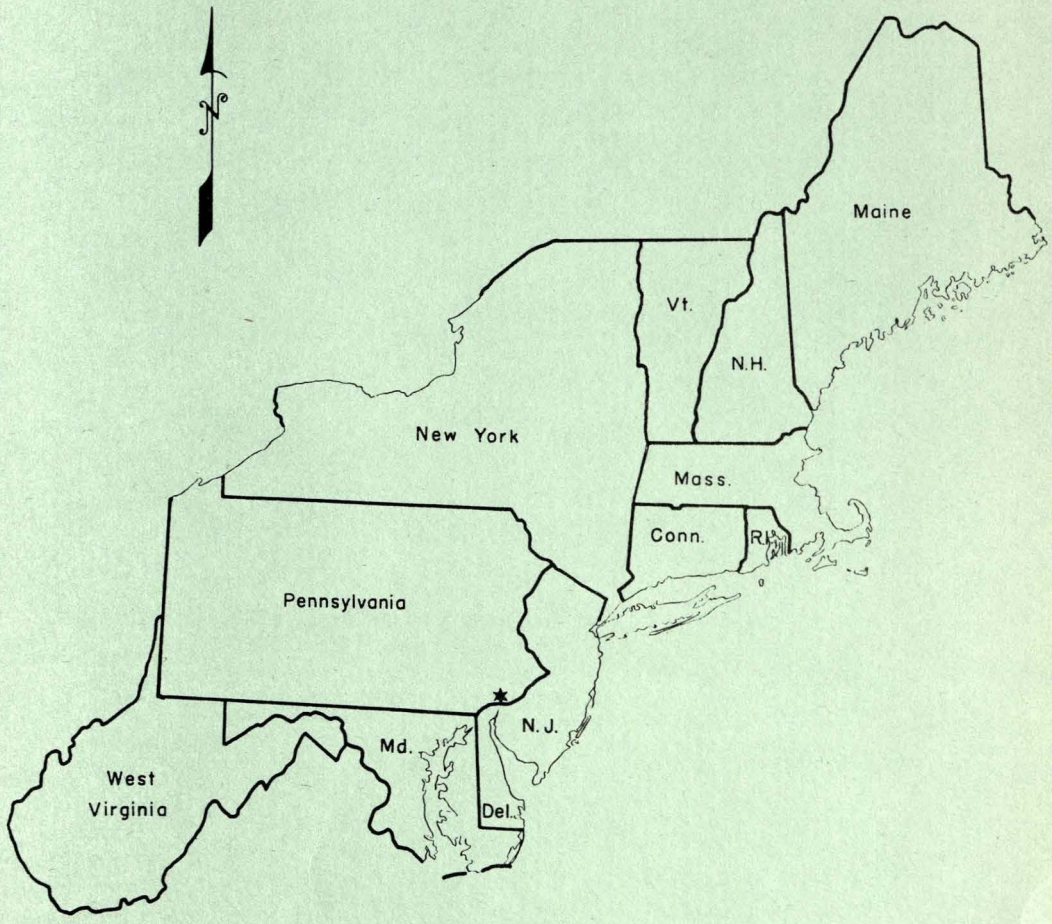

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